DENDROECOLOGICAL INVESTIGATION OF RED-COCKADED WOODPECKER CAVITY TREE SELECTION IN ENDANGERED LONGLEAF PINE FORESTS

A Thesis
by
APRIL L. KAISER

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Abstract

DENDROECOLOGICAL INVESTIGATION OF RED-COCKADED WOODPECKER CAVITY TREE SELECTION IN ENDANGERED LONGLEAF PINE FORESTS

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The red-cockaded woodpecker (RCW) is a keystone species that thrives in longleaf pine savanna forests. Using standard tree-ring science techniques, we collected and analyzed core samples from longleaf pine trees in the Sandhills Gameland Reserve in North Carolina selected by RCW for their cavities (RCWC) and adjacent control trees (RCWCo) and explored differences in climate/growth response and radial growth disturbance events in these two groups. We developed RCWC and RCWCo tree-ring chronologies that allowed us to explore the possibility that climate vulnerability is a component of the RCW selection process for their nests. Specifically, we investigated climate/growth responses, radial growth suppressions, and physical characteristics of both tree types through a comparison of diameter at breast height (DBH), tree age, latewood band width, and frequency of resin ducts (1950–2018). For long-term climate response (1910–2018), we found no significant differences between RCWC and RCWCo trees. However, we identified significant differences in climate/growth relationships between RCWC and RCWCo through time-series analysis with significant differences in the number of suppression events and spatially grouped suppression events. For tree physiology, we found significantly more resin duct

from 1950–2018 in RCWC trees. Our tree-ring based examination addressed multiple factors in why RCWs select specific longleaf pine trees for cavities. This additional understanding may help improve conservation efforts for RCW and longleaf pine throughout their ranges.

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I am in great debt to all my dedicated thesis advisors, Dr. Peter Soulé, Dr. Saskia van de Gevel, and Dr. Paul Knapp. I would not have been able to complete this thesis without their incredible support. I would also like to acknowledge my fellow dendro-researchers in the amazing Appalachian Tree-Ring Lab: Bri Hibner, Julia Adams, and Rebecca Sigafoos. They always made me keep a positive attitude throughout the day and helped support me throughout the stages of my thesis. I also cannot articulate my gratitude to my fellow graduate student cohort who never failed to make me laugh and push me in my academic career. I could also never forget to thank Austin Lassiter, Petra van de Hey, my family, and my wonderful furry children who helped me overcome any hurdle that came my way.

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Dedications

I dedicate this thesis to my incredibly supportive family, human and animal alike, and all who have helped me to, “speak for the trees, for the trees have no tongue.” -Dr. Seuss

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Foreword

The main body of this thesis is formatted to the guidelines for manuscript submission to *Endangered Species Research*, an official journal of the Inter-Research Science Center.

Introduction

Red-cockaded woodpecker (*Leuconotopicus borealis;* RCW) are the only known woodpecker species to use live-pine cavities to build their nests, raise their young, and roost at night (Ligon 1970). Although RCW will use various southern pines, longleaf pine (*Pinus palustris*) are their preference (Lennartz & Henry 1985). With nesting cavity excavation taking anywhere from one to several years, protection of their selected high-quality trees is crucial to their survival (Jackson et al. 1979). Because of this high energy cost to build their cavities, RCWs will typically remain at the same nesting site for years unless drastic changes occur to their location (Ligon 1970, Lay et al. 1971, Jackson 1978, personal communication, Brady Beck).

Historic longleaf pine range initially stretched throughout most of the southeast, ranging anywhere from eastern Texas to southern Virginia. Today, over 98% of previous longleaf pine habitat has been eradicated with only 1,376,000 hectares present in 2010 (https://www.nrcs.usda.gov/wps/portal/nrcs/detail/national/programs/financial/rcpp/?cid=stelprdb1254129). This decline was caused by a combination of human development, fire suppression, and timber industry actions, which have led to the endangered conservation status for longleaf pine (Landers et al. 1995, Outcalt & Sheffield 1996, Wear & Greis 2002, Frost 2007, Farjon 2013, U.S. Fish and Wildlife Service 2018). Due to RCW's dependence on longleaf pine, their populations also were negatively impacted and they are recognized as a federally endangered species (Lennartz & Henry 1985). While there are many studies focused on RCW cavity tree selection mechanisms, to our knowledge ours is the first to incorporate traditional tree-ring science methodologies (Locke et al. 1983, Field & Williams 1985, Hooper 1988, Rudolph & Conner 1991, Loeb et al. 1992, Ross et al. 1997). This new perspective has the potential to help improve conservation management techniques for both endangered species.

We specifically focused on whether RCW cavity trees were more climate-sensitive, if they had more growth suppressions, and if they had different physical characteristics in comparison to control trees that did not have cavities. These three aspects were chosen due to literature gaps on climate sensitivity differences between tree categories, tree ring growth suppressions in cavity trees using running-mean and running-median analysis, and inconsistent results found in physical characteristics of cavity trees (Conner & O'Halloran 1987, DeLotelle & Epting 1988). Understanding these factors in cavity trees and if there is a significant difference from control trees can help answer how resilient these trees may be with future environmental pressures, changes, and insect outbreaks. Additionally, these findings can help conservation managers better protect more susceptible trees and determine how future environmental impacts may affect RCW populations as well.

During my junior year of my undergraduate career, I took an ornithology course that visited the Sandhills region in North Carolina. There, my class and I tracked down RCW in the Pisgah National Forest, which primarily consists of longleaf pine. This experience made me realize how beautiful longleaf pine savanna forest could be. During my first year of my masters program, I had an opportunity to continue working with longleaf pine and wanted to incorporate my roots in wildlife biology with my new-found passion in tree-ring science. I achieved this by completing a dendroecological investigation of RCW cavity trees. My co-authors and I acquired historical cores initially collected by Dr. Jeffrey Walters from Virginia Tech around 1980. However, due to these cores being nearly 40 years old and how much climate has changed in the last 38 years, we pursued collection of new data from the same study site. To do this, we attained a permit from the North Carolina Wildlife Resource Commission officer, Brady Beck. This document allowed me, my thesis advisors, and another student to collect new tree data from Sandhills Gameland, NC.

Our climate analysis used the R package, 'treeclim' to investigate long-term climate/growth correlations and time-series analyses between my two chronologies, cavity (RCWC) and control (RCWCo). This process had not been attempted using RCW cavity trees before. Our suppression analysis used the R package 'TRADER' to determine suppressions in tree-ring growth using parameters to filter out climate impacts. Conner and O'Halloran (1987) examined suppression and release patterns in tree ring growth in RCW cavity trees. However, their methodology did not use 'TRADER' or our filtering parameters and was completed in a different geographic region. Our examination of tree characteristics helped determine if there are physical differences in the cavity trees in comparison to the control trees for our study site. Our main objective was to provide new information to the North Carolina Wildlife Resource Commission in Sandhills Gameland to help aid management strategies for protection of both endangered species.

The roles of each of the authors are as follows: 1) April Kaiser developed the research questions, conducted all of the literature reviews, directed the field sampling, processed all of the data in the laboratory, ran analyses discussed with thesis advisors, and wrote the thesis document 2) Peter Soulé assisted with the field sampling, was the primary advisor for statistical analyses, and was the primary editor of the manuscript, 3) Saskia van de Gevel assisted with the field sampling, assisted with the R programming and analysis of suppression events, and was a secondary editor, 4) Paul Knapp assisted with the field sampling, provided reference chronologies, assisted with the crossdating, and was a tertiary editor, 5) Arvind Bhuta provided the previously mounted and sanded historical cavity tree cores, 6) Jeffrey Walters initially cored the historical cores and provided guidance on RCW behavior and how it associated with our results, 7) Evan Montpellier aided in program troubleshooting and quality control.

Dendroecological investigation of red-cockaded woodpecker cavity tree selection in endangered longleaf pine forests

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ABSTRACT

Old-growth longleaf pine (*Pinus palustris*) is a keystone/foundation species for 29 threatened or endangered species in the coastal plain of the southeastern United States. The endangered red-cockaded woodpecker (*Leuconotopicus borealis*; RCW) and endangered longleaf pine have an established ecological association. Here, we explore differences in climate/growth response and radial growth disturbance events in trees with RCW cavities compared to non-cavity trees in the Sandhills Gameland Reserve in North Carolina, USA. Using standard dendrochronological techniques, we collected and analyzed core samples from the trees selected by RCW for their cavities (RCWC) and adjacent control trees (RCWCo) that had no visible cavity. We developed RCWC and RCWCo tree-ring chronologies that allowed us to examine if climate vulnerability is a component of the RCW selection process for their nests. Specifically, we investigated climate/growth responses, radial growth suppressions, and physical characteristics of both tree types through a comparison of diameter at breast height (DBH), tree age, and frequency of resin ducts. For long-term climate response (1910–2018), we found no significant differences between RCWC and RCWCo trees. However, we identified temporal differences in climate/growth relationships between RCWC and RCWCo with significant differences in the number of suppression events and spatially grouped suppression events. For tree physiology, we found more resin ducts during 1950–2018 in RCWC trees. Our dendroecological-based investigation examines multiple factors in addressing the question of why RCWs select specific longleaf pine trees for cavities, which may help improve conservation efforts for RCW and longleaf pine.

KEY WORDS: red-cockaded woodpecker, longleaf pine, dendroecology, climate/growth sensitivity, ecological disturbance

1. INTRODUCTION

Longleaf pine (*Pinus palustris*) and red-cockaded woodpecker (*Leuconotopicus borealis;* RCW) species reside throughout the southeastern United States. Although RCW use additional southern pines for foraging and nesting cavities, such as loblolly pine (*Pinus taeda*), old-growth longleaf pine is their preference (Lennartz & Henry 1985). These woodpeckers require a tree cavity for each within the complex social structure of a woodpecker family (Walters et al. 1988). RCW and longleaf pine are listed as endangered by the U.S. Fish and Wildlife Service and have a declining population trend (Farjon 2013, U.S. Fish and Wildlife Service 2018). The RCW conservation status is attributed to longleaf pine decline during the 1800s– mid-1900s (Lennartz & Henry 1985). Longleaf pine historically ranged across 37.2 million hectares throughout the southeastern United States (Frost 1993, Landers et al. 1995). The current distribution has decreased to less than 1.2 million hectares due to fire suppression, timber industries, urban development, agriculture, and habitat fragmentation (Landers et al. 1995, Outcalt & Sheffield 1996, Wear & Greis 2002, Frost 2007). RCWs depend on old-growth longleaf pine to create their cavities, with selected pine age averages ranging from 49–171 years (Hovis & Labisky 1985).

RCWs use live-pine cavities to build their nest and raise fledglings (Ligon 1970). With nesting cavity excavation ranging from one to several years, protection of their selected trees is crucial for their survival (Jackson et al. 1979). Because of high energy expenditure to build their cavities, RCWs will typically remain at the same nesting site for 5-10 years unless drastic changes occur to their nesting location (Ligon 1970, Lay et al. 1971, Jackson 1978, personal communication, Brady Beck). With individual RCW territory requirements of 50–125 hectares and an established cluster requirement of 50,000 hectares, each potential cavity or foraging tree is essential for the future survival of the species (Zwicker & Walters 1999).

Ornithologists and forest ecologists have explored which tree characteristics RCWs prefer for building cavities (Ligon 1970, Locke et al. 1983, Field & Williams 1985, Hooper 1988, Rudolph & Conner 1991, Loeb et al. 1992, Ross et al. 1997, Hooper et al. 1999, Zwicker & Walters 1999). RCW are known to select pines that are older than 60 years and wider than 25 cm with trees older than 100 years most preferred (Zwicker & Walters 1999). Tree selection is also positively associated with heartwood decay (Hooper et al. 1991). This decay can be facilitated by the presence of red heart fungus (*Phellinus pini*), which makes cavity excavation easier (Walters 1991). Longleaf pine cavity trees are known to have an intermediate level of stress and the highest resin flow rates (Ross et al. 1997). These traits could aid in predator deterrence with increased sap at the entrance of the cavities and are typically located along the forest edge (Jackson 1974, Rudolph et al. 1990, Ross et al. 1997). Although characteristics of trees selected by RCW for their nests (cavities) are well-documented (Locke et al. 1983, Field & Williams 1985, Hooper 1988, Rudolph & Conner 1991, Loeb et al. 1992, Ross et al. 1997) the RCW selection mechanism has contradictory results (Conner & O'Halloran 1987, DeLotelle & Epting 1988). In this study, we investigated this mechanism further through analysis of differences in climate sensitivity, ecological disturbances, and longleaf pine tree physiologic characteristics between cavity (RCWC) and non-cavity (control; RCWCo) longleaf pines. We hypothesized that RCWC trees would be more sensitive in climate/growth relationships, in temporal climate/growth analysis, and have more suppression events due to the presence of cavities and the impacts from cavity excavation. Additionally, we predicted that RCWC trees would be larger in DBH, older, have more resin ducts, and have wider latewood bands than RCWCo trees.

2. MATERIALS AND METHODS

2.1. Study Area

We collected all tree cores at Sandhills Gameland (SGL), a protected nature reserve maintained by the North Carolina Wildlife Resources Commission (NCWRC) (Fig. 1.). The Sandhills region has a temperate climate with an average annual precipitation of 116.8 cm and annual mean temperature averaging 16.8 °C (North Carolina Wildlife Resources Commission 2015). SGL spans across both the National Oceanic and Atmospheric Administration (NOAA) climate divisions 5 and 6 (Fig. 1.; National Oceanic and Atmospheric Administration). Initially owned by private investors and named the Broad Acres Plantation in the early 1900s, SGL was obtained by the Department of Defense in 1942. An airborne training facility, Camp Mackall, was established during World War II. Post-war, SGL became North Carolina state land on May 19th, 1948 with NCWRC assuming wildlife management duties in the 1950s. Historically, the economy of the Sandhills region consisted of agriculture, forestry, and textile industries. Agricultural lands were primarily abandoned in the 1970s and 80s and bought by timber companies. Textile industries have declined, leaving the area to consist of primarily forestry management corporations (North Carolina Wildlife Resources Commission 2015). These changes facilitated the North Carolina Sandhills Conservation Partnership (NCSCP) to form in 2000 and created successful cooperation between conservation groups for the region’s federally endangered longleaf pine (North Carolina Sandhills Conservation Partnership 2018). The collaboration also aides 29 federally listed endangered species found in the longleaf pine savanna habitat such as RCW, Cooley's Meadowrue (*Thalictrum cooleyi*), Eastern Indigo Snake (*Drymarchon corais couperi*), and Gopher Tortoise (*Gopherus polyphemus*) (Lennartz & Henry 1985, North Carolina Sandhills Conservation Partnership 2018). NCSCP's efforts towards the conservation and recovery of RCW have been successful in conserving RCW habitat (North Carolina Wildlife Resources Commission 2015). According to NCWRC, a near-fully recovered population of RCWs exists at SGL (personal communication, Brady Beck). This increased strength of the RCW population in SGL provided us with a unique opportunity, through NCWRC approval, to take core samples from RCW-cavity trees. Taking samples from trees with active RCW cavities is typically not permitted within managed RCW ecosystems because of low population levels and land manager concerns about disturbing nesting bird populations.

2.2. Data Collection

We collected core samples from 27 RCWC longleaf pine trees at breast height from complete and naturally excavated RCW cavity trees. RCWC trees were located in defined clusters throughout SGL, with each cluster designating an RCW social group. A tree identification tag number marked each RCWC tree, and the NCWRC maintains detailed records for each of these trees. We also collected samples from 33 RCWCo longleaf pines. For the RCWCo trees, we used a selective sampling strategy whereby we sampled a minimum of one tree in proximity (i.e., within 200 m radius) of the RCWC tree and with similar physiological characteristics. Thus, all RCWCo trees were mature trees with similar heights and diameters at breast height (DBH). For all trees, we used increment borers to obtain a minimum of two cores samples at breast height. Additionally, we recorded diameter at breast height (cm), GPS coordinates, and observable tree characteristics for all trees sampled.

2.3. Climate Data

For analyses of the climate/growth relationships, we used monthly average temperature, monthly total precipitation, and monthly average Palmer Drought Severity Index (PDSI; Palmer 1965) variables from the National Oceanic and Atmospheric Association (NOAA) Physical Sciences Division data portal (www.esrl.noaa.gov/psd/data/timeseries/) for the period 1910–2018 (NOAA 2019). We determined climate division data were most reliable because averaged climate data are a more accurate representation for a region and are more strongly related to tree-ring growth (Blasing et al. 1981). As SGL straddles the boundary between two climate divisions, we conducted a preliminary correlation analysis and found stronger relationships between radial growth and Climate Division 6 data and proceeded with Climate Division 6 data.

2.4. Chronologies

We created separate chronologies for the RCWC and RCWCo trees. We used standard dendrochronological procedures to process the tree-ring core samples in the lab (Stokes & Smiley 1996). We glued each core sample to a wooden mount with cells vertically aligned, then sanded the sample until the cellular structure was clean under magnification. We crossdated the core samples using the list method (Yamaguchi 1991) in association with a previously developed tree-ring chronology from Uwharrie National Forest, NC (Mitchell et al., 2019). We scanned the cores samples to 1,200 dots per inch (DPI) resolution and digitally measured each sample using WinDendro (version 2017a). We verified crossdating accuracy was verified using COFECHA (Holmes 1983) with 50-year segments lagged successively by 25 years. When COFECHA identified problems, we re-dated the core samples to correct those errors.

The RCWC chronology included the cores we collected in 2019 and 11 historically archived cores that were included in a cavity tree chronology initially collected by in 1980 and 1981 by Dr. Jeffrey Walters. Both chronologies are based on latewood widths, which are more closely related to climatic conditions than total wood widths for longleaf pine (Henderson & Grissino-Mayer 2009, Patterson et al. 2016). Our RCWCo chronology had two "A" flags identified by COFECHA and included 30 core samples. Our RCWC chronology had zero flags identified and also included 30 core samples. The RCWC tree chronology had a mean interseries correlation of 0.552 and a mean sensitivity of 0.455; the RCWCo chronology had a mean interseries correlation of 0.539 and a mean sensitivity of 0.457. COFECHA takes the composite chronology and calculates and removes individual tree ring series Pearson correlation coefficients, and then takes an overall average to reach a mean interseries correlation value (Grissino-Mayer 2001). Mean sensitivity is a climate sensitivity indicator determined by the relative differences among individual tree ring sizes (Fritts 1976).

We standardized radial growth using the computer program ARSTAN and Friedman's Super Smoother method with a tweeter sensitivity set to five (Cook & Holmes 1984, Friedman 1984). Standardization is needed to remove individual tree age-related growth trends (Cook & Holmes 1984). Friedman's Super Smoother is an adaptive, non-parametric, smoothing regression technique used to preserve low-frequency variance (Friedman 1984). We obtained the highest mean series intercorrelations using this standardization method, which allows the highest climate/growth correlations to occur (Hart et al. 2010). Once ARSTAN outputs were created, we ensured the chronologies attained an expressed population signal (EPS) of ≥ 0.85. EPS indicates solidity of sample depth (Wigley et al. 1984, Duchesne et al. 2017). An EPS of ≥ 0.85 was reached in 1910 for both RCWC and RCWCo using a 10-year overlap with 5-year running window. For both RCWC and RCWCO, we created new variables that adjust the latewood chronologies for the influence of earlywood on tree growth (Meko & Baisan 2001).

2.5. Statistical Analysis

We performed a Shapiro-Wilks test and a Kolmogorov-Smirnoff test using the 'stats' package in R and the 'shapiro.test' and 'ks.test' functions, respectively. We used both tests to check normality as a Shapiro-Wilks normality is one of the most powerful normality tests but was initially made for small sample sizes (Shapiro & Wilk 1965, Razali & Wah 2011, Maes et al. 2017, R Core Team 2017). Therefore, we supplemented with a Kolmogorov-Smirnoff test to ensure the correctness of distributions. We also performed a Bland-Altman analysis using the 'BlandAltmanLeh' R package function, 'bland.altman.stats' to determine differences between chronologies and if related bias occurred (Bland & Altman 1986, Bland & Altman 1999, Lehnert 2014). We performed a Spearman's Ranked Correlation test using the 'stats' package in R and then 'cor.test' function to determine the strength of covariance between chronologies (R Core Team 2017).

We analyzed climate/growth relationships for both the RCWC and RCWCo chronologies and two individual trees from the same cluster using the R package 'treeclim' (Zang & Biondi 2015). Using the 'dcc' function in treeclim, we determined classical bootstrapped correlations between both chronologies and monthly average PDSI, monthly total precipitation, and monthly average temperature climate variables from previous May through current December from 1910–2018. We used the Fisher r-to-z transformation test to determine if significant differences existed in the strength of the primary climate/growth relationships between RCWC and RCWCo trees. We tested for the possibility that climate/growth relationships have differed between RCWC and RCWCo adjusted latewood chronologies through time using classical bootstrapped 25-year moving correlation analysis from previous May through current December from 1910–2018 using the same three climate variables (Biondi & Waikul 2004, Zang & Biondi 2015). We performed a one-tailed z-test for independent proportions on the percent of significant coefficients for all moving interval correlations between RCWC and RCWCo. We then compared a RCWC tree with a neighboring RCWCo tree using non-standardized totalwood chronologies using 25-year moving correlation windows.

We used the R package 'TRADER' to identify ecological disturbances on individual trees (Altman et al. 2014). We used annual raw totalwood measurements (1910–2018) from each sample (n = 30) for both RCRW and RCRCo chronologies (total n = 60). We used a radial-growth averaging method, the 'growthAveragingALL' function in 'TRADER', as it produced fewer Type I and Type II errors and had a lower deductive data requirement (Nowacki & Abrams 1997, Trotsiuk et al. 2018). Through this analysis, we determined individual tree growth suppressions using all 60 trees from the chronologies with three parameters. First, we identified moderate suppressions if there was a 25–50% growth change and major suppressions if there was a greater than 50% growth change. Second, a seven-year length minimum was required for any suppression event. Third, suppression events were required to be at least 10 years apart (Nowacki & Abrams 1997). We selected these parameters to filter climate and fire-related suppressions (Stambaugh et al. 2011, Maes et al.

2017). We ran this growth change analysis using both the running-mean method and the running-median method because there is a non-parametric growth pattern found in trees (Rubino & McCarthy 2004, Hart et al. 2008).

We detected overall suppression events during 1910–2018. We created a composite figure of all suppressions for both suppression detection methods (running-mean and median methods) and visually compared the temporal pattern to the pattern of the climate/growth relationship derived from both moving interval correlations. We determined small scale spatial groupings of suppression events in RCWC and RCWCo trees based on three criteria. First, three or more trees needed to be involved in the group. Second, trees involved in suppression groups were required to be < 1,000 m apart. Third, a minimum of four suppressions were required. For our ecological disturbance statistical difference analysis, we performed one-tailed and two-tailed Wilcoxon Rank Sum Tests on the number of suppressions detected per tree ($n = 60$) to determine if a significant difference ($p < 0.1$) was present between tree types. We also compared the total number of suppressions detected per tree between running-mean and running-median, using a one-tailed and two-tailed Wilcoxon Signed Rank Test ($n = 60$). We plotted NOAA's Climate Division 6 annual average PDSI from 1910–2018 (www.esrl.noaa.gov/psd/data/timeseries/) to determine if suppression events coincided with drought in RCWC and RCWCo trees (Figure 9; NOAA 2019)

We explored the physical characteristics of both RCWC and RCWCo longleaf pines to determine if any significant differences were present. We determined tree age using only complete tree record cores that included bark to near pith (13 RCWC; 27 RCWCo). We estimated missing rings to pith with a comparison of ring-width patterns and the aid of pith locator diagrams (Duncan 1989). We counted the number of resin ducts in the latewood bands (where they primarily occur) during 1950–2018 for 30 RCWCo cores and 19 RCWC. We did not include 11 RCWC trees that were from the historically archived data due to the years ending in 1980 or 1981. DBH data included all sampled trees (27 RCWC trees; 33 RCWCo trees). We tested for significant differences between RCWC and RCWCo trees in DBH ($n = 60$), the number of resin ducts (1950–2018; $n = 49$), and raw (i.e., non-standardized) latewood width differences ($n = 60$) using one-tailed and two-tailed Wilcoxon Rank Sum Tests as data were non-normal. We conducted one-tailed and two-tailed independent samples *t*-tests for the normally distributed tree age data ($n = 40$).

3. RESULTS

3.1. Chronologies

Shapiro-Wilks tests determined RCWC was non-normally distributed with a bimodal curve ($p < 0.05$) and RCWCo was normally distributed with a unimodal curve ($p > 0.05$) (Fig. 2). Additionally, we found no significant difference between RCWC and RCWCo standardized radial growth ($p > 0.05$). We also did not find any long-term growth trends in either standardized chronology (Fig. 2). Our Bland-Altman analysis at a 95% confidence interval found a mean difference of 0.00036 mm, with the greatest standardized width difference in 1911 (0.44 mm). We found a strong correlation coefficient of 0.859 ($p < 0.001$) between RCWC and RCWCo chronologies.

3.2. Climate/Growth Analysis

We found that RCWC and RCWCo responded similarly to average monthly PDSI, total monthly precipitation, and average monthly temperature (Table 1). Both chronologies had significant positive relationships with PDSI from July–December, with RCWC significance beginning one month earlier in June (Table 1; Fig. 4). RCWC had the strongest relationship with current October PDSI ($r = 0.418$; $n = 108$) and RCWCo with current September PDSI ($r = 0.389$; $n = 108$). PDSI is a water balance-based measure of drought severity (Palmer 1965). Thus, it incorporates both supplies of moisture (i.e., precipitation) and potential demand through evapotranspiration (i.e., temperature).

We determined that summer and fall precipitation had significant positive relationships with growth for RCWC and RCWCo (Fig. 4). Average monthly temperature had non-significant relationships with both chronologies except a positive relationships with May temperature for both chronologies and a negative relationship with August temperature for RCWCo. Previous months had little to no impact on current-year growth for all climate variables (Fig. 4). Comparatively, monthly climate variables of the current year had the most impact, and longleaf pine respond positively with wet summer and fall conditions. Although RCWC generally exhibited slightly stronger relationships with climate than RCWCo, for all monthly comparisons we found no significant differences in R-values based on the Fisher r-to-z transformation test.

3.3. Temporal Climate/Growth Analysis

Moving-correlation analysis shows similar trends and relationships in both RCWC and RCWCo chronologies for all three climate variables (Fig. 5; Table 2). PDSI had a significantly positive relationship with radial growth through time during June–December. In comparison, prior months illustrate mostly negative relationships. We identified a divergence effect in the RCWC previous months that began in the 1957–1981 moving interval and ended in the 1977–2001 interval. The same divergence was not as substantial in the RCWCo trees. RCWC also had a stronger and more significant relationship with PDSI than RCWCo ($p < 0.01$; Table 2).

Precipitation had similar patterns to PDSI through time for both chronologies (Fig. 5b). Current months had a positive trend while previous year's months were typically negative. Wet summers and autumns had a positive effect on growth for both RCWC and RCWCo chronologies. Additionally, previous dry summers had an overall negative effect on ring growth for both chronologies with a more negative effect for RCWC (Fig. 5). We found a similar divergence effect using precipitation to the one we found with PDSI in both RCWC and RCWCo. We found positive, strong, and significant ($p < 0.05$) climate/growth relationships with precipitation in June, July, September, and October (Fig. 5b). However, RCWC positively associates more with wet conditions than RCWCo and has a notable drop in climate signal around 1965. RCWC had a consistently positive relationship for February, but RCWCo was not temporally stable. We found overall occurrence percentages to have no significant difference between RCWC and RCWCo for precipitation/growth through time (Table 2).

We discovered that the overall weak relationship between radial growth and average temperature might be related to the instability of these relationships through time (Fig. 5c). We found RCWCo to be more responsive to temperature than RCWC (Table 2). However, average temperature's inverse relationship with PDSI emphasizes a stronger relationship between precipitation and growth. Therefore, PDSI, which uses both precipitation and temperature, has a stronger precipitation driver than temperature.

We found differences in PDSI moving interval correlation analysis on individual raw totalwood chronologies from an RCWC (Tree ID: SGR21A) and adjacent RCWCo tree (Tree ID: SGC27A; Fig. 6). We found SGC27A had a higher frequency of significant correlation coefficients ($p < 0.01$; Fig. 6). Both trees grew more in wet conditions than dry (Table 3). However, when dry conditions did occur, SGR21A was more negatively impacted than SGC27A. Additionally, when conditions were wet, SGC27A grew more than SGR21A. We detected two divergence events in SGC27A from a positive relationship to negative. In comparison, we found three divergence events in SGR21A. Our findings of differences between this paired sample of RCWC and RCWCo trees led to our next investigation of whether RCWC trees have different patterns of radial growth suppression potentially related to the physical process of cavity excavation by RCW relative to RCWCo trees.

3.4. Ecological Disturbance

Our running-mean suppression analysis detected a total of 43 moderate suppressions in the RCWC trees and 36 in the RCWCo trees. Additionally, we found 29 major suppressions in RCWC trees and 24 in RCWCo trees. RCWC trees had more suppressions overall and more major suppressions than RCWCo trees ($p < 0.1$, $p < 0.1$; $n = 30$; Table 4). However, there was no difference in moderate suppression totals for RCWC and RCWCo trees (Table 4). There were no stand-wide major, moderate, or combined suppression events, with the three highest amounts of overall suppression events occurring in 1964, 1961, and 2001 with 18.3%, 16.7%, and 15% of trees affected, respectively (Fig. 7; $n = 60$; Nowacki & Abrams 1997, Rubino & McCarthy 2004). We did find a severe drought occurred in 2002, which was only one year after a large suppression event (Fig. 7).

We found small spatial scale groupings of suppression events for both RCWC and RCWCo trees for both running-mean and running-median methods (Fig. 7, 8). For running-mean analysis, we found four small-scale groups for RCWC trees and two for RCWCo trees (Fig. 7). From 1937 to 1940, group A had seven major or moderate suppression events. Two trees are from the same cluster, while the other four were from an adjacent cluster about 70 meters away. Group B had eight suppression events in a 5-year period from 1961–1966, including a historical core denoted as group b (Fig. 7). Three trees were in the same cluster about 16 meters apart while the other three were in another cluster ≤ 800 meters away. In 1982, group C had five events that involved four trees and were all located in the same cluster. Seven suppression events occurred in group D from 1997–2001 and all but one tree were in the same cluster. In comparison, RCWCo trees only had two small spatial scale groups. We found four trees all in the same cluster, group E, during 1974 and 1975 that had four suppressions. Group F suppressions occurred in 2000 and 2001 involved three trees with four suppressions in the same cluster (Fig. 7). We did not find any groups to occur during or after drought. However, we did find three groups (A, D, F) that preceded drought by one year.

Our running-median suppression method detected the same amount of moderate suppressions for both RCWC and RCWCo trees, 32 events. We identified 30 major suppressions for RCWC while RCWCo only had 21. We found a distinct difference in major suppressions between the RCWC and RCWCo trees ($p < 0.10$; $n = 30$; Table 5). Additionally, RCWC trees had significantly more major suppression events than RCWCo trees ($p < 0.05$; $n = 30$; Table 5). We did not find any stand-wide suppressions for major, moderate, or overall suppression events (Nowacki & Abrams 1997, Rubino & McCarthy 2004). The three highest percentages of trees affected were 15%, 13.3%, 13.3% in 1982, 1964, and 1961, respectively (Fig. 8).

Although no stand-wide disturbances occur, a smaller spatial scale also appears with the median-running analysis (Fig. 8). We detected the same number of groups for both running-mean and running-median analyses. For RCWC trees, group A had six suppressions from 1936–1940 in three trees from one cluster and two from another around 800 meters away. We found that group B had eight suppression events between years 1961 and 1965. Three trees involved were in one cluster while four were in another about 800 meters away. In 1982, six events occurred in group C with four trees in the same cluster and one, again, only 800 meters away. From 1997–2001, five suppressions occurred in group D. All trees except one were in the same cluster with the other tree located ≤ 800 meters away. RCWCo trees had two groups. Group E occurred from 1970–1973, had five suppressions, and were in the same cluster. Our other group for RCWCo trees, group F, had four suppressions from 1995–1998 and were also in the same cluster (Fig. 8). Two groups, B and C, occurred during large suppressions. All groups did not coincide with any drought event (Fig. 8). However, two groups, A and D, preceded a drought event by one year.

We found significant differences between running-mean and running-median analysis types for moderate and overall suppression totals per tree ($p < 0.01$; $n = 60$; Table 6). We also found significantly more moderate and overall suppressions in running-mean analysis than running-median analysis ($p < 0.01$; $n = 60$; Table 6). We did not find any differences in running-mean and running-median detection for major suppressions. We found that no drought events preceded large suppressions from 1910–2018 (Fig. 7, 8).

3.5. Tree Characteristics

We found no significant differences between RCWC and RCWCo for diameter at breast height (DBH), age, and latewood width. We did find that RCWC had significantly more resin ducts (1950–2018) than RCWCo ($p < 0.05$; Fig. 10; Table 7).

4. DISCUSSION

4.1. Chronologies

We found RCWC and RCWCo chronologies to be complementary with only a few discrepancies. The bimodal distribution for RCWC is non-normally distributed, but this is not uncommon for biological processes (Rubino & McCarthy 2004). However, our Bland-Altman analysis showed a mean radial growth difference of only 0.00008 mm, thus we found no significant difference in long-term radial growth between RCWC and RCWCo. The greatest difference we found between the two chronologies was 0.44 mm in 1911, which coincides with a severe drought event (Fig. 8). However, other differences that were close in value (i.e., 0.41 mm in 1989) did not occur with a drought event. These contradictory findings may be related to drought resilience or the sensitivity to water table depth and overall water availability (Foster & Brooks 2001, Ford et al. 2008, Henderson & Grissino-Mayer 2009, Samuelson et al. 2012, Knapp et al. 2016). Additionally, we posit that these results could indicate a more localized disturbance event such as fire or RCW cavity excavation.

4.2. Climate/Growth Analysis

PDSI was initially created to aid in drought detection (Palmer 1965, Dai et al. 1998, Dai 2011) and has been shown to have a strong association with longleaf pine and various tree species throughout the southeastern United States (Grissino-Mayer & Butler 1993, Foster & Brooks 2001, Henderson & Grissino-Mayer 2009, Hart et al. 2010, Patterson et al. 2018, Mitchell et al. 2019). Our climate/growth correlation analysis found the longleaf pine cavity and control trees responded most favorably to wet, cool conditions. Strong relationships occurred throughout current summer and fall seasons for both chronologies (Fig. 4), and there were no significant differences ($p > 0.05$) between the RCWC and

RCWCo relationships with PDSI in any month based on the Fisher r-to-z transformation test. Additionally, our correlation coefficients are consistently > 0.3 with no strong lag effect on current-year growth. Longleaf pine did not show a relationship with previous year's PDSI or precipitation values (Cook & Jacoby 1977, Henderson & Grissino-Mayer 2009).

Precipitation is often one of the most influential climate factors for longleaf pine growth (Foster & Brooks 2001, Sayer & Haywood 2006, Henderson & Grissino-Mayer 2009, Patterson et al. 2016, Mitchell et al. 2019), and this sensitivity has allowed for longleaf pine to be used for climate reconstructions such as tropical cyclone precipitation (Knapp et al. 2016). Current June and July precipitation ($r > 0.2$) for RCWC had the highest impact on tree growth similar to the relationships we found with PDSI during summer. While February precipitation can be an essential driver of longleaf pine radial growth (Henderson & Grissino-Mayer 2009), our results reveal a weak, positive relationship for February (Fig. 4). While there are fewer significant monthly relationships for precipitation compared to PDSI, we found no significant differences between the RCWC and RCWCo trees for all months using the Fisher r-to-z transformation test.

We found PDSI to be the most significant climate variable that impacts longleaf pine radial growth at SGL. Mean monthly temperature is not closely aligned with radial growth of longleaf pine at SGL, with only two months producing significant relationships (Fig. 4). Although longleaf pine typically has a strong positive association with precipitation (Foster & Brooks 2001, Bhuta et al. 2009, Patterson et al. 2016, Mitchell et al. 2019), our results show that in this location, the combined impact of temperature and precipitation recorded in the PDSI are more closely aligned with radial growth. Soil moisture supply during the current summer and fall directly impacts longleaf pine radial growth. Overall, our climate/growth results suggest that our hypothesis of RCWC being more climate-sensitive on a long-term time scale (i.e., 1910–2018) is not supported.

4.3. Temporal Climate/Growth Analysis

Temporal stability of climate/growth relationships is critical for dendroclimatology studies (Wilson & Elling 2004). Climate response consistency is vital for accurate predictions of global carbon cycle changes (Briffa et al. 1998a, Briffa et al. 1998b). Our long-term climate/growth correlation results suggest that both RCWC and RCWCo trees respond similarly to climate. However, when using the shorter 25-year intervals in our moving-interval analyses, we found that RCWC had considerably more significant relationships than RCWCo for PDSI and less for average temperature (Fig. 5a, 5b; Table 2). While our analyses do not reveal why this occurs, we postulate there may be some physiological differences (e.g., resin ducts) between RCWC and RCWCo trees that cause RCWC to be more susceptible to evapotranspiration and better suited for cavity construction, or that some aspect of the cavity excavation process and presence makes them more sensitive to drought. Our study site history could also aid in understanding this phenomenon. SGL management uses prescribed fires at 1-3-year fire intervals, which has a direct impact on longleaf pine growth and stand dynamics (Binkley et al. 1992, Brockway & Lewis 1997, Van Lear et al. 2005, Lavoie et al. 2010). Disturbance events, such as RCW cavity excavation, impact climate sensitivity (Fritts 1976), which would likely exacerbate the switch in climatic response and create additional divergence events.

Overall patterns for PDSI show a significantly positive and static relationship with radial growth through time for current year growth, but growth in the previous year clearly shows a shift in the climatic signal (Fig. 5a). We found a substantial divergence effect for the previous year's months in both chronologies with RCWC again having a more significant presence (Fig. 5a; Table 2). In the context of climate change, anomalous temperature increases could negatively impact longleaf pine through decreasing water availability in the clay and sandy soils found in the region (Iverson et al. 2008) and may have an association with teleconnections impacts on large-scale weather patterns (Leathers et al. 1991). Additionally, these oscillations directly impact fire regimes by changing weather patterns and the scheduling of prescribed fires (Pielke & Landsea 1999, Yocom et al. 2010). Changes in fire regimes can allow mid-story development that introduces more interspecific competition and predators to RCWs and allow southern pine beetle outbreaks to occur which impact cavity trees more (Conner et al. 1991, Conner & Rudolph 1991, Conner & Rudolph 1995, Loeb et al. 1992, Waldrop et al. 1992, Loudermilk et al. 2011).

Little knowledge exists for how cavity excavation impacts trees except that cavity trees have more resin flow and that geographic context influences cavity tree susceptibility (Hansell 1993, Ross et al. 1997). Although SGC27A had more overall significance than SGR21A and SGC27A grew more during wet conditions (Fig. 6), SGR21A is more negatively impacted by dry conditions. We posit that SGR21A's vulnerability to dry conditions could be due to cavity presence in the tree. Our moving-interval correlation analysis on an individual tree scale illustrated more divergence events in the RCWC tree than the RCWCo tree (Fig. 6). While these events could be caused by fire events or microenvironmental impacts such as blight or southern pine beetle outbreaks (Kalkstein 1976, Snow et al. 1990), a more likely explanation is that the divergence is temporally associated with the cavity excavation process. Overall, we cannot support our hypothesis that RCWC are more climate sensitive to precipitation and average temperature. However, we can support that RCWC are more sensitive to PDSI and that overall patterns of climate/growth relationships through time may differ on an individual scale.

4.4. Ecological Disturbance

We found RCWC trees to have significantly more suppression events than RCWCo trees for our running-mean analysis ($p < 0.1$; Table 4). Our running-median analysis found more major suppression events in RCWC trees than RCWCo trees ($p < 0.05$; Table 5), and we presume that this is directly related to the stressors imposed on trees during the period of cavity excavation. While we did not find any stand-wide suppressions (>25% of trees affected; Rubino & McCarthy 2004), we found one event that affected 18.3% of the trees, which suggests a possible stand-wide event occurred in 1964. This large-impact event could potentially be related to a high-intensity fire or a silvicultural event in this calendar year. The 7-year suppression minimum and 10-year gap between suppressions likely filtered out some fire-caused suppression. However, longleaf pine does have extensive fire-resistant defenses that could have influenced suppression detection sensitivity (Andrews 1917, Chapman 1932, Heyward 1939, Wahlenberg 1946, Croker & Boyer 1975, Platt et al. 1988, Platt et al., 1991, Platt 1999). For example, eastern Texas longleaf pine cavity trees have notable suppression and release events (Conner & O'Halloran 1987). Although this finding used methods for suppression and release detection based on a growth rings/cm measurement for > five years, our usage of the more extensive quantitative Nowacki and Abrams (1997) method found a similar result (Rentch et al. 2002, Hart et al. 2008, Altman et al. 2016, Abiyu et al. 2018). Suppressions we found in both RCWC and RCWCo trees had different small-scale spatial patterns. We propose two possible explanations for the small spatial groupings to occur. First, we propose that the affected cluster(s) were all suppressed by the same microenvironmental factors. Second, we suspect that the affected cluster(s) were trees suppressed by RCW cavity excavation. Additionally, both analyses found small-scale spatial groups in the 1960s and late 1990s/early 2000s for both RCWC and RCWCo trees. Due to this similarity, we postulate that these two suppressions are not due to RCW excavation of cavities. However, the 1982 event occurred only in RCWC trees, which could mean RCWs created cavities that suppressed growth. Additionally, in groups A and C for both analyses, drier conditions occurred (negative PDSI) that might have caused carbon starvation, which potentially make trees easier to excavate. This water stress also causes increased phloem sap viscosity, which RCW prefer (Wallin et al. 2003, McDowell et al. 2008, Woodruff 2013). Carbon starvation occurs when there is a lack of photosynthesis due to the closure of stomata, which prevents hydraulic failure, thus mortality of the tree (McDowell et al. 2008).

Running-median analysis has been shown to be better adapted for biological growth (Rubino & McCarthy 2004, Hart et al. 2008). Both analyses found significance in different suppression types (Table 4, 5). We found that running-mean analysis found significantly more suppression events than running-median for both moderate and overall suppressions ($p< 0.01$; Table 6). Additionally, our yearly stand-wide percentages varied between the two methods. Our running-median method did not detect as large of suppressions as running-mean. We believe the running-median analysis is not well suited for detection of synchronous events. These significant variations ($p < 0.01$) support the usage of running-mean analysis to ensure no suppressions are undetected. We found more major and overall suppression events for RCWC trees, which allows us to support our hypothesis that RCWC trees have more suppressions.

4.5. Tree Characteristics

We found significantly more ($p < 0.05$) resin ducts in RCWC trees from 1950–2018 (Fig. 10, Table 7), which concurs with prior findings on RCW tree selection (Ross et al. 1997). Ponderosa pine that survived bark beetle attacks have significantly more carbon investment in resin ducts than those that did not survive (Kane & Kolb 2010). This finding could explain why RCWC trees had more resin ducts based on two ideas. First, RCWs select longleaf with more resin ducts because of their increased resistance to bark beetle outbreaks (Santoro et al. 2001, Nowak et al. 2008). Second, RCWs choose trees that have more resin ducts because of the increased resin flow when these birds create predator deterrent resin wells around a cavity entrance (Rudolph et al. 1990). All other physical characteristics were not significantly different (Table 7). RCW cavity trees are typically larger in DBH and older in age than non-cavity trees (Jackson et al. 1979, Conner & O'Halloran 1987, Rudolph & Conner 1991). However, age may not be critical to RCW cavity tree selection (Field & Williams 1985). RCW selection factors could also differ depending on management practices (James et al. 1997), and SGL has been carefully managed with frequent prescribed burns since the late 1990s (North Carolina Wildlife Resources Commission 2015).

5. CONCLUSION

Our study is the first, to our knowledge, to use dendroecological analyses to examine differences between trees that the endangered red-cockaded woodpecker selects for their nesting cavities, and nearby control trees with visually similar physiological characteristics that RCW did not select. RCWs require a cavity for each bird to roost and nest. (Ligon 1970, Walters et al. 1992). Creation of these cavities creates stability in an environment, which supports a carrying capacity-level population (Horn 1978). With this association, abandonment of a cavity becomes more difficult, which thereby adds support for RCW cooperative breeding behavior (Horn 1978, Hansell 1993). When cavities are abandoned, they are still highly sought after by other endangered species (Lennartz & Henry 1985, North Carolina Sandhills Conservation Partnership 2018). Without these cavities, RCWs will not survive, and neither will the species dependent on their cavities (Ligon 1970, Jackson 1977, Lennartz & Henry 1985).

We used dendroecological methods to investigate why these trees were selected for cavities and if they were more vulnerable to climate variables and disturbance events. First, we did not find significant differences between RCWC and RCWCO for long-term climate/growth relationships. Second, we did not find differences in the physiologic characteristics of tree age, DBH, or width of latewood bands. However, we did find three distinctions between tree chronologies and tree types. First, we found that significant climate signals shift through time between RCWC and RCWCo climate/growth relationships and also might differ on an individual tree scale. Second, we found that RCWC trees experienced more frequent suppression events than RCWCo trees. Third, we found that resin ducts were more prevalent in RCWC trees than RCWCo trees. We also found that running-mean analysis produced significantly more suppression detections than running-median analysis. Our results show that RCWC trees are more sensitive to climate than RCWCo trees over shorter intervals and that the process of cavity construction likely results in more frequent radial growth suppressions. If a period of suppressed growth was concurrent with a climatic event like an extreme drought, the possibility exists that RCWC trees would be more susceptible to senescence (Sayer & Haywood 2006, Rivero et al. 2007). While there are radial growth differences between RCWC and RCWCo trees, we do not have consistent enough results to suggest that RCWC trees are more susceptible to environmental pressures such as severe drought, fire, or southern pine beetle outbreaks. However, we discovered that RCW cavity excavation potentially causes stress-induced suppressions. Therefore, management practices could emphasize precautions for trees that have cavity-starts during high-intensity fires and periods of dryness, which could help mitigate suppression of growth and possible mortality. We also determined that running-mean analysis detected more suppressions using our parameters and should be used for future tree-ring disturbance studies.

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Table 1. Most significant ($p < 0.05$) climate/growth relationships (r) by month

Type	RCWC	RCWCo
PDSI	October (0.418)	October (0.378)
Precipitation	June (0.269)	July (0.368)
Average Temperature	May (0.172)	August (-0.209)

Table 2. Time-series analysis percentages of significant correlations between RCWC and RCWCo with monthly PDSI, average temperature, and precipitation variables between years 1910 and 2018. P values (n = 1700) from a one-tailed z-test for independent proportions between RCWC and RCWCo chronologies

Climate Variable	Type	Significant Percentage	p value
PDSI	RCWC	21.88%	**$p < 0.001$*****
	RCWCo	16.82%	
Precipitation	RCWC	13.29%	$p = 0.2058$
	RCWCo	12.35%	
Average Temperature	RCWC	6.76%	**$p = 0.0749$***
	RCWCo	8.01%	
***=significance at 90% confidence interval; **= significance at the 95% confidence interval; ***=significance at 99% confidence interval**			

Table 3. P values from one-tailed z-test of independent proportions for all comparisons between percentages of significantly negative and significantly positive correlations of the RCWC tree example (SGR21A) and RCWCo tree example (SGC27A). Sample size is the number of significant months in the moving interval years

Type	Significantly Negative (%)	Significantly Positive (%)	p value	Sample Size
RCWC Tree (SGR21A)	41.60	58.40	**$p < 0.0001$*****	n = 113
RCWCo Tree (SGC27A)	7.40	92.60	**$p < 0.0001$*****	n = 162
p value	**$p < 0.0001$*****	**$p < 0.0001$*****		
*****=significance at 99% confidence interval**				

Table 4. P values of Wilcoxon Rank Sum Tests of moderate, major, and all suppressions using running-mean analysis between RCWC and RCWCo trees

Type of Suppression	Type of Wilcoxon Rank Test	p value	Sample Size
Moderate	RCWC ≠ RCWCo	p = 0.2138	n = 60
	RCWC < RCWCo	p = 0.8931	n = 60
	RCWC > RCWCo	p = 0.1069	n = 60
Major	RCWC ≠ RCWCo	p = 0.1604	n = 60
	RCWC < RCWCo	p = 0.9198	n = 60
	RCWC > RCWCo	**p = 0.08021***	n = 60
All Suppressions	RCWC ≠ RCWCo	p = 0.1821	n = 60
	RCWC < RCWCo	p = 0.9090	n = 60
	RCWC > RCWCo	**p = 0.09104***	n = 60
***=significance at 90% confidence interval**			

Table 5. P values of Wilcoxon Rank Sum tests of moderate, major, and all suppressions using running-median analysis between RCWC and RCWCo trees

Type of Suppression	Type of Wilcoxon Rank Test	p value	Sample Size
Moderate	RCWC ≠ RCWCo	p = 1.0000	n = 60
	RCWC < RCWCo	p =0.50310	n = 60
	RCWC > RCWCo	p = 0.50310	n = 60
Major	RCWC ≠ RCWCo	**p = 0.07389***	n = 60
	RCWC < RCWCo	p = 0.9631	n = 60
	RCWC > RCWCo	**p = 0.03694****	n = 60
All Suppressions	RCWC ≠ RCWCo	p = 0.2495	n = 60
	RCWC < RCWCo	p = 0.8752	n = 60
	RCWC > RCWCo	p = 0.1248	n = 60
***=significance at 90% confidence interval **=significance at 95% confidence interval**			

Table 6. P values of Wilcoxon Signed Rank tests of moderate, major, and all suppressions between running-mean (Mean) and running-median (Median) analysis types. Analysis was paired between the same RCWC trees and the same RCWCo trees

Type of Suppression	**Type of Wilcoxon Signed Rank Test**	**p value**	**Sample Size**
	Mean = Median	**p = 0.007051*****	n = 60
	Mean < Median	p = 0.9965	n = 60
Moderate	Mean > Median	**p = 0.003525*****	n = 60
	Mean = Median	p = 0.6547	n = 60
	Mean < Median	p = 0.6726	n = 60
Major	Mean > Median	p = 0.3274	n = 60
	Mean = Median	**p = 0.004681*****	n = 60
	Mean < Median	p = 0.9977	n = 60
All Suppressions	Mean > Median	**p = 0.002341*****	n = 60
***=significance at 90% confidence interval **=significance at 95% confidence interval ***= significance at 99% confidence interval**			

Table 7. Wilcoxon Rank Sum Test for DBH (cm), Resin Ducts (1950–2018), and latewood width (mm) and t-test for age p values between RCWC and RCWCo trees.

Characteristic	**Strongest Relationship**	**p value**	**Sample Size**
DBH	RCWC > RCWCo	$p = 0.50000$	$n = 60$
Resin Ducts	RCWC > RCWCo	**$p = 0.01908$****	$n = 49$
Latewood Width	RCWC < RCWCo	$p = 0.11500$	$n = 60$
Age	RCWC < RCWC	$p = 0.22030$	$n = 40$
***=significance at 90% confidence interval **=significance at 95% confidence interval**			

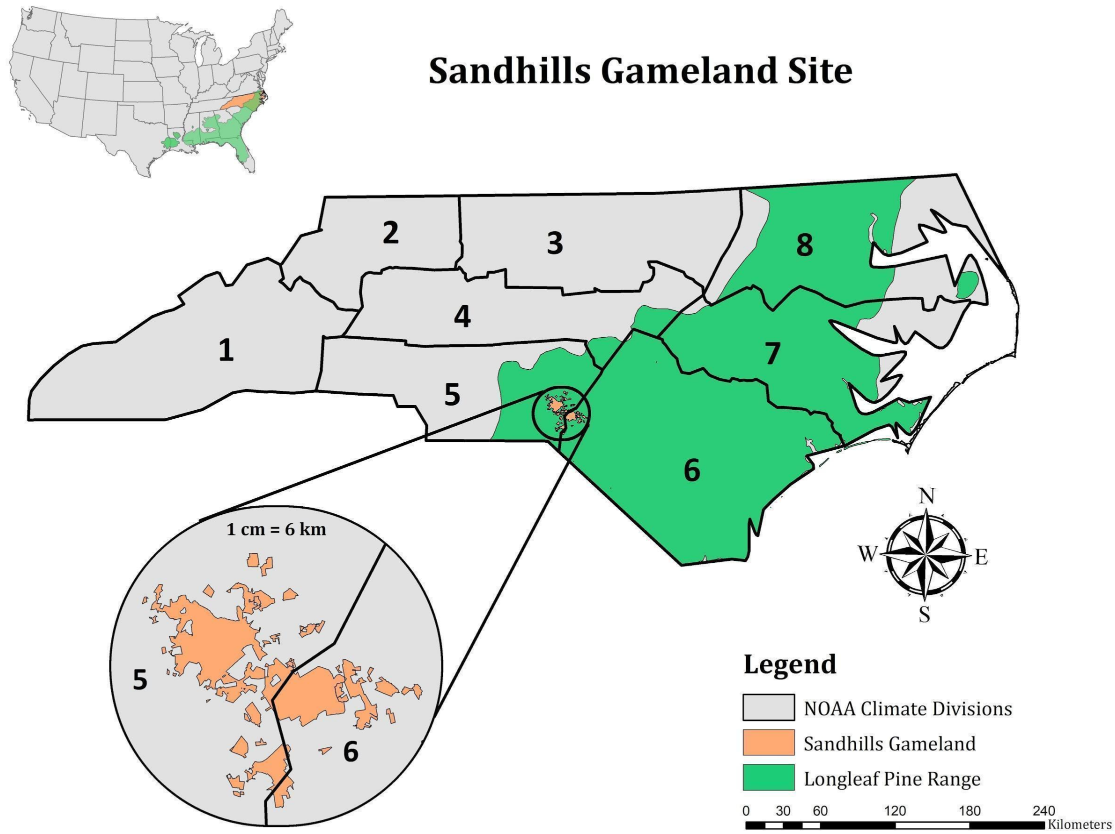

Fig. 1. North Carolina with NOAA climate divisions, spatial extent of the Sandhills Gameland (orange), and current range of Longleaf pine (U.S. Department of Agriculture, 2014)

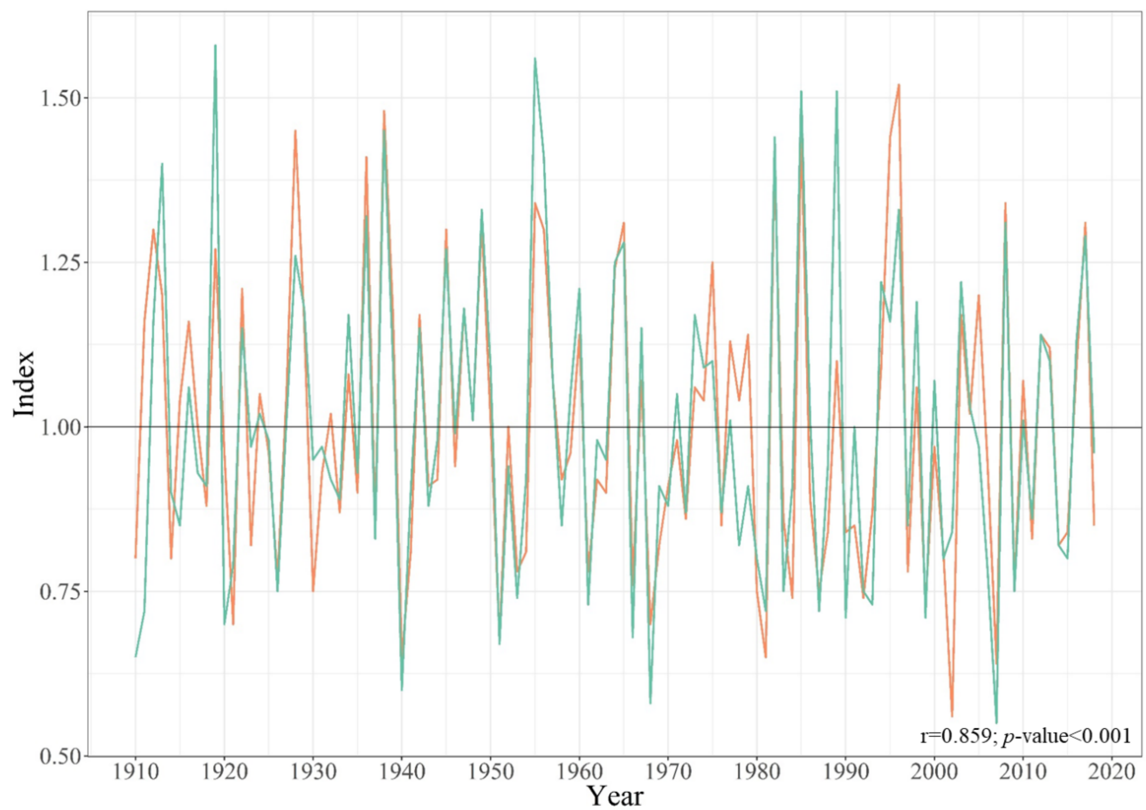

Fig. 2. Ring-width index between cavity (orange) and control (green) adjusted latewood chronologies. Correlation coefficient for Spearman correlation was significant (r = 0.859; p < 0.001). Black line denotes the average index for both chronologies

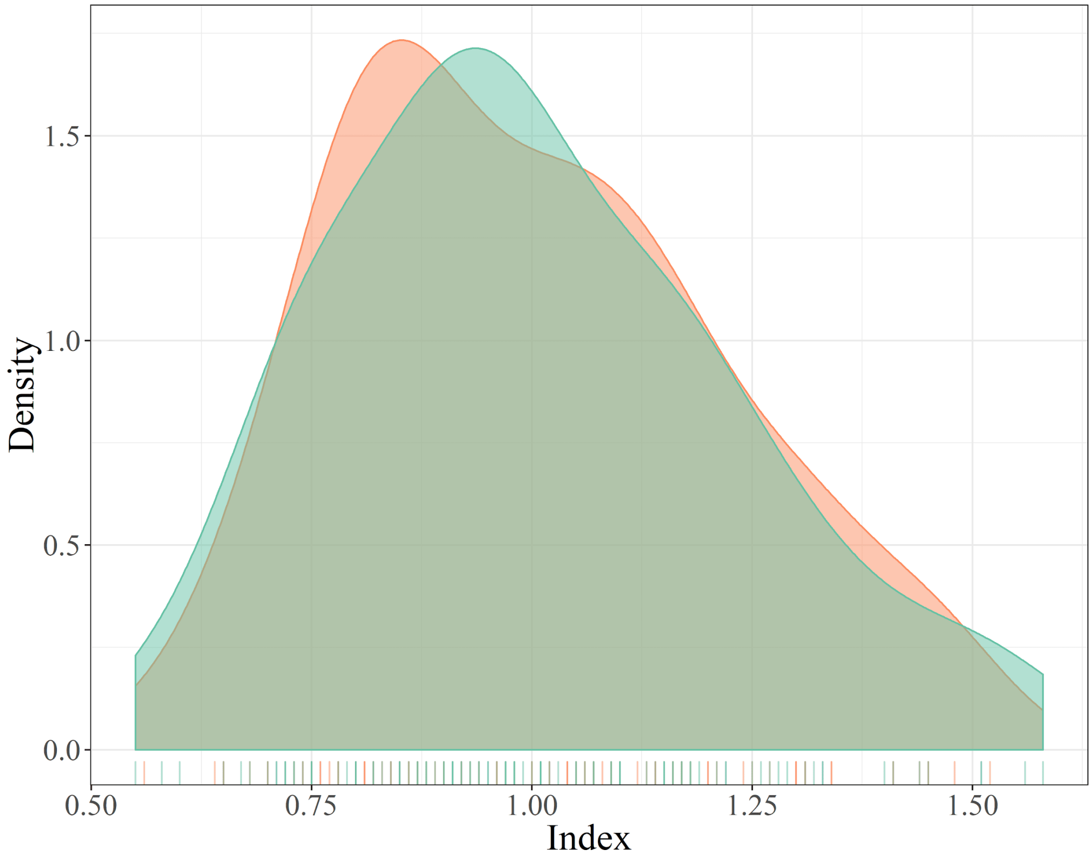

Fig. 3. Density plot of bimodal and non-normally distributed RCWC (orange) and unimodal and normally distributed RCWCo (green) adjusted latewood chronologies

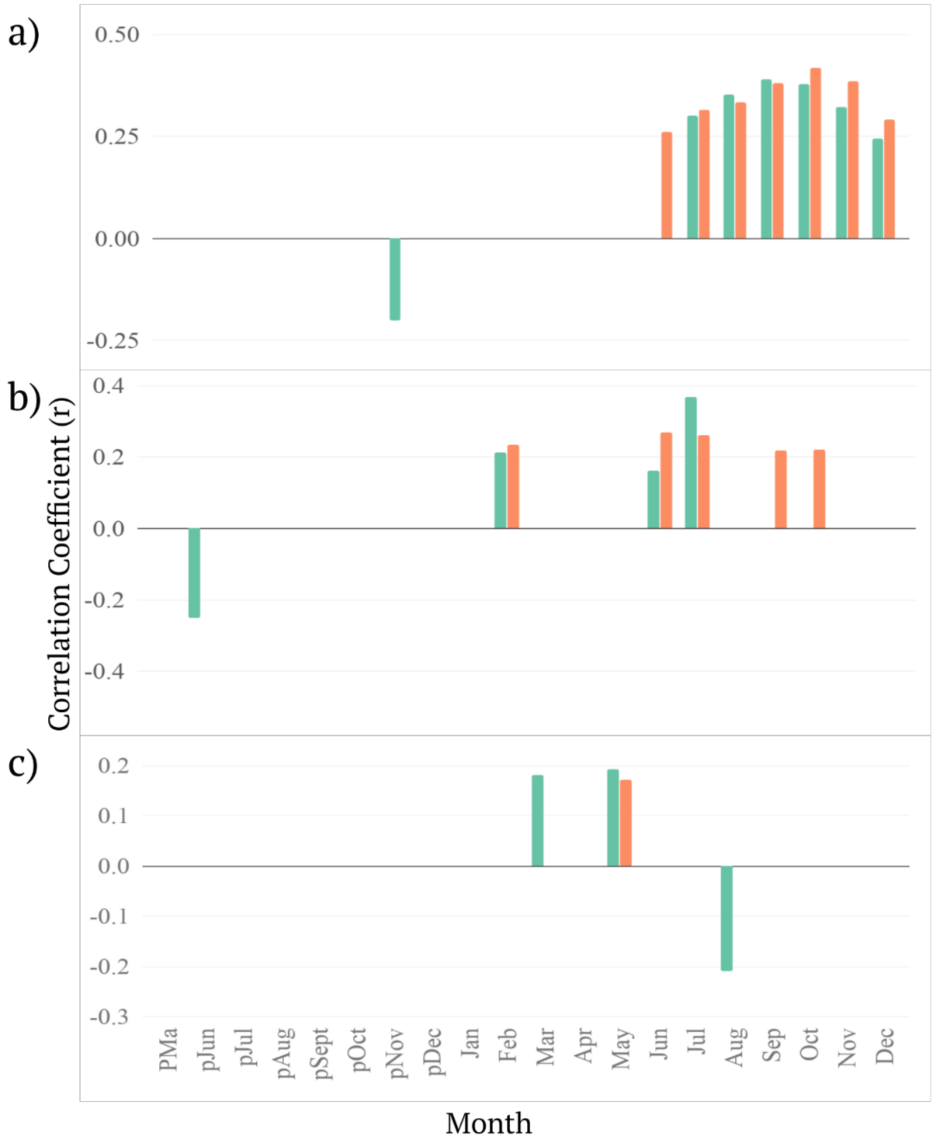

Fig. 4. Significant climate/growth relationships between 1910–2018 (r value) of RCWC (orange) and RCWCo (green) with a) average PDSI, b) total precipitation, and c) average temperature. A month starting with 'p' denotes a previous year's month

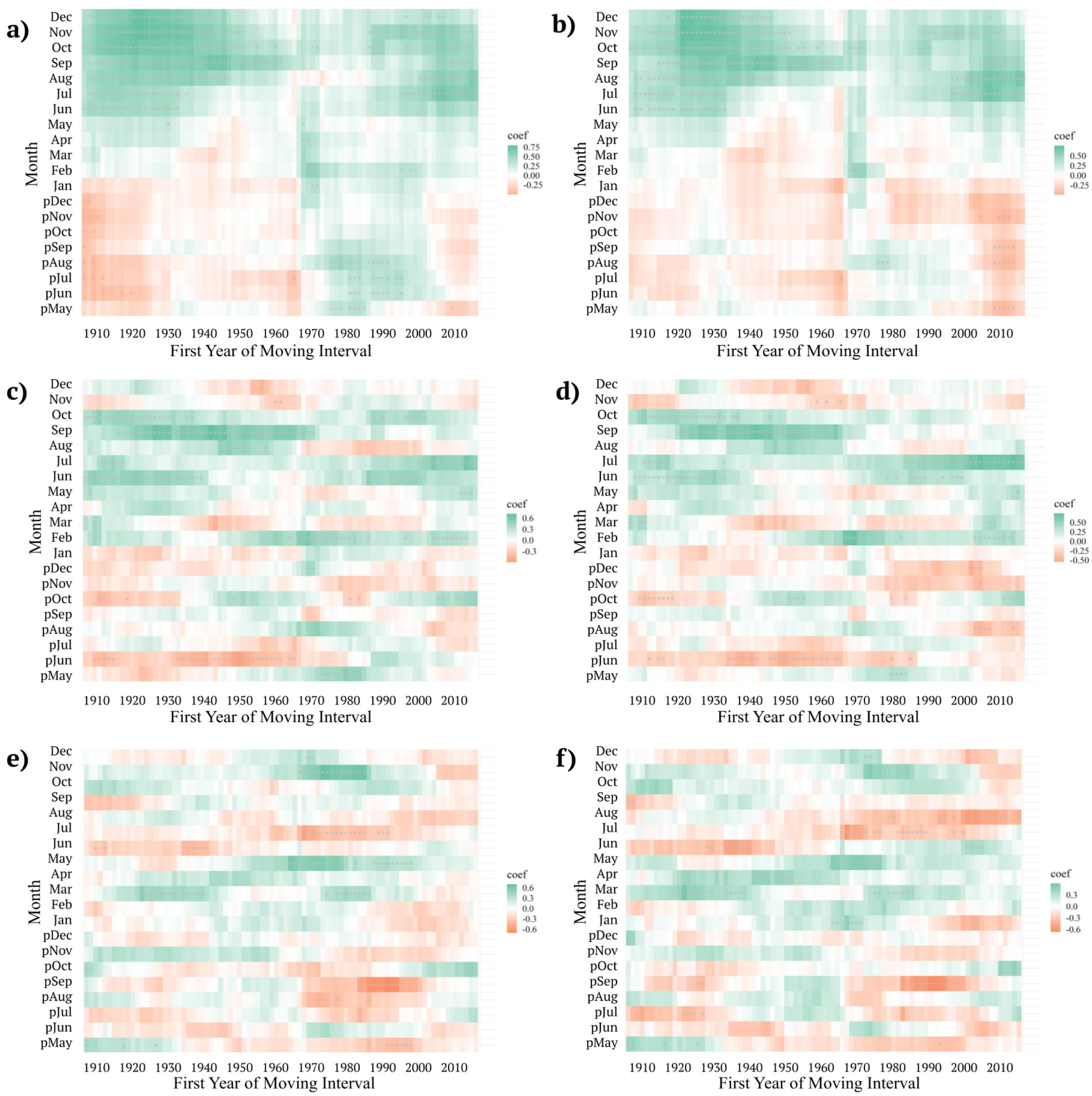

Fig. 5. Moving interval correlations for a) RCWC with average monthly PDSI b) RCWCo with average monthly PDSI, c) RCWC with total monthly precipitation, d) RCWCo with total monthly precipitation, e) RCWC with monthly average temperature, and f) RCWCo with monthly average temperature average monthly. Green indicates positive correlation coefficients (coef; r) while orange indicates negative correlation coefficients (coef; r), grey asterisks indicate a significant interval ($p < 0.05$), and ‘p’ indicates a previous year’s month

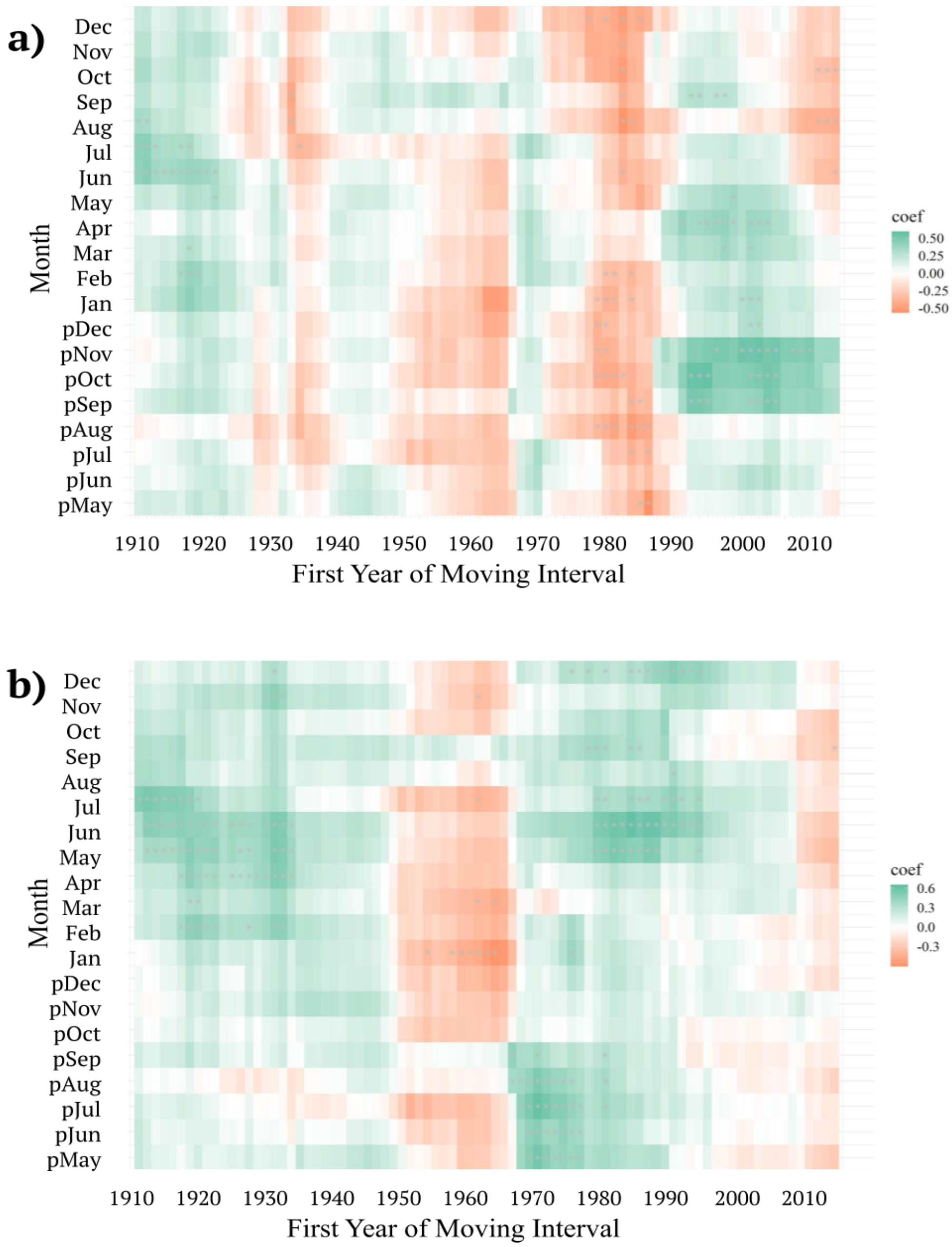

Fig. 6. Moving interval correlation PDSI analysis for a tree from a) RCWC (SGR21A) and b) RCWC (SGC27A). Green indicates positive correlation coefficients (coef; r) while orange indicates negative correlation coefficients (coef; r) and grey asterisks indicate a significant interval ($p < 0.05$). RCWC tree had 6.81% significant values and RCWCo tree had 9.76% and are significantly different at the 99% confidence interval ($p < 0.01$)

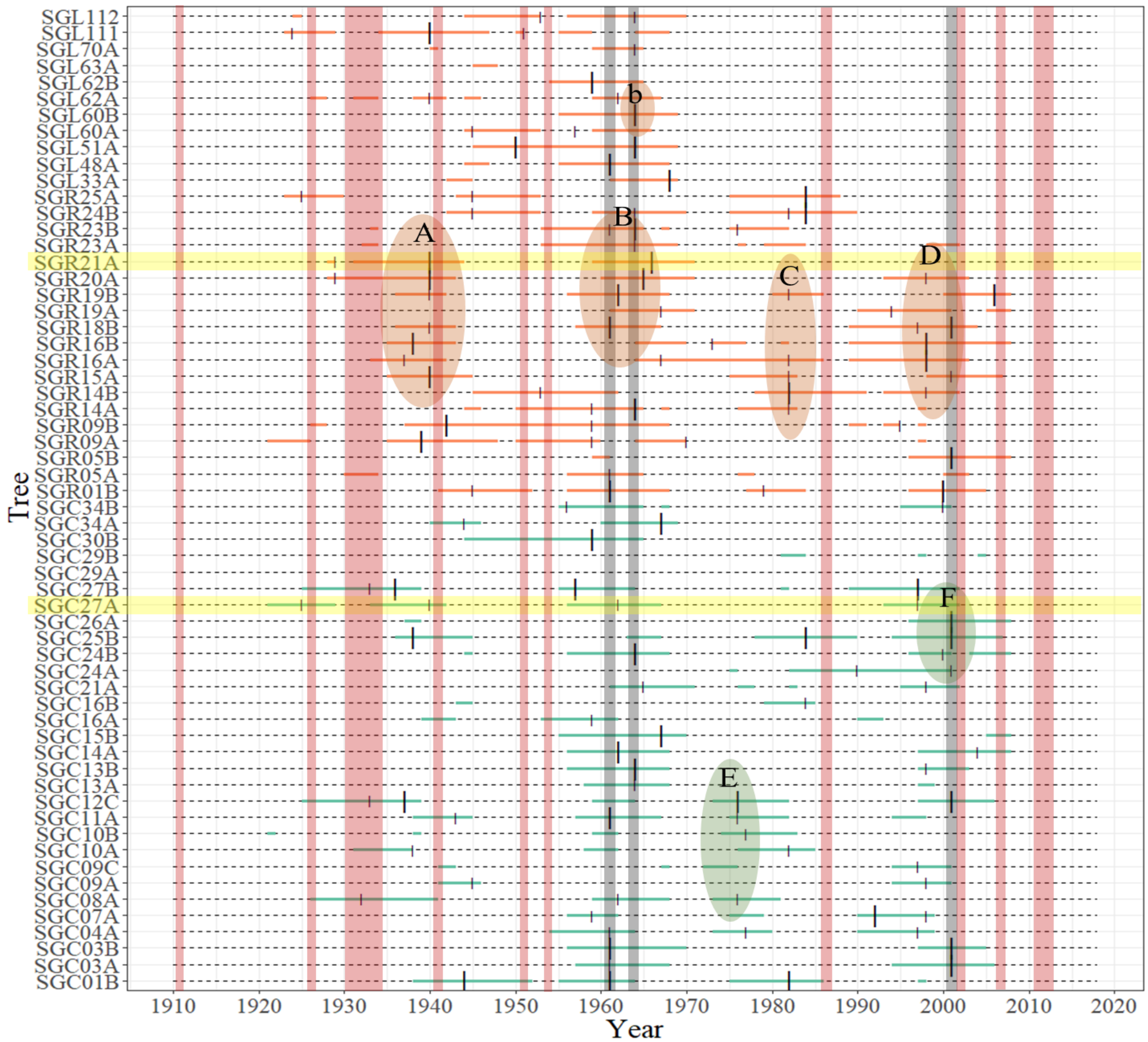

Fig. 7. Running-mean analysis with RCWC and RCWCo trees. Major suppression events are long tick marks (>50% growth change, suppression length >7 years, gap between suppressions >10 years) and moderate suppression events are short tick marks (<50% and >25% growth change, suppression length >7 years, gap between suppressions >10 years) with suppressed growth denoted by color orange bars are RCWC trees with prefix SGR or SGL (historic), green bars are RCWC trees with prefix SGC; A and B signifies either the first or second core sampled from the tree. Grey boxes indicate 1961, 1964, and 2001, the three years with the highest percentage of trees impacted at 16.7%, 18.3%, and 15.0%, respectively. Red box highlights are periods of drought (Dai & National Center for Atmospheric Research Staff 2017). Circles and letters illustrate smaller spatial scale groupings of major or moderate suppressions for RCWC trees (orange) and RCWCo trees (green). One circle labeled for a single suppression event, b, is associated with the larger group, B. Yellow highlights are the RCWC tree (SGR21A) and RCWCo tree (SGC27A)

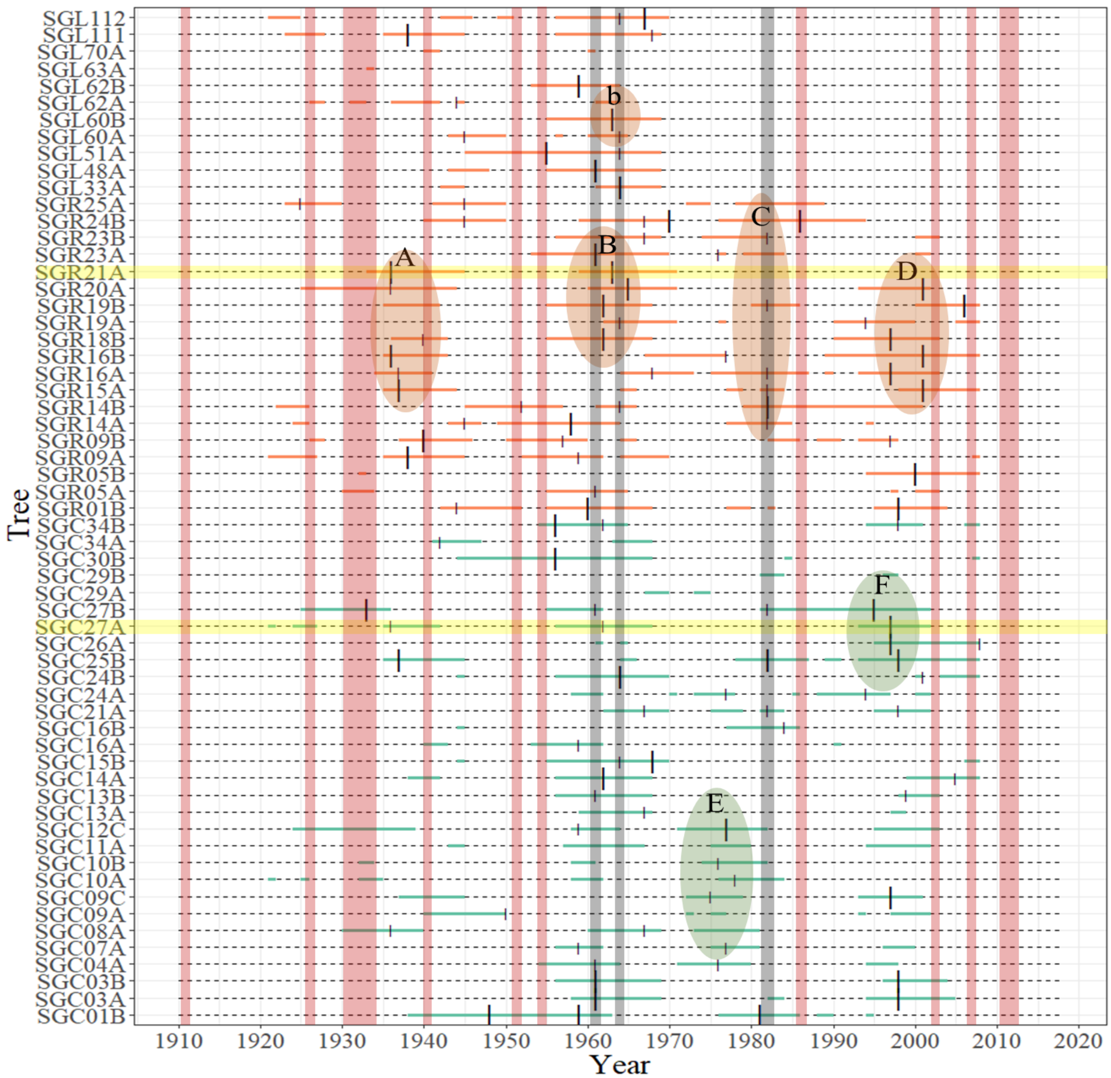

Fig. 8. Running-median analysis with RCWC and RCWCo trees. Major suppression events are long tick marks (>50% growth change, suppression length >7 years, gap between suppressions >10 years) and moderate suppression events are short tick marks (<50% and >25% growth change, suppression length >7 years, gap between suppressions >10 years) with suppressed growth denoted by color orange bars are RCWC trees with prefix SGR or SGL (historic), green bars are RCWC trees with prefix SGC; A and B signifies either the first or second core sampled from the tree. Grey boxes indicate 1961, 1964, 1982, the three years with the highest percentage of trees impacted at 13.3%, 13.3%, and 15%, respectively. Red box highlights are periods of drought (Dai & National Center for Atmospheric Research Staff 2017). Circles and letters illustrate smaller spatial scale groupings of major or moderate suppressions for RCWC trees (orange) and RCWCo trees (green). One circle labeled for a single suppression event, b, is associated with the larger group, B. Yellow highlights are the RCWC tree (SGR21A) and RCWCo tree (SGC27A)

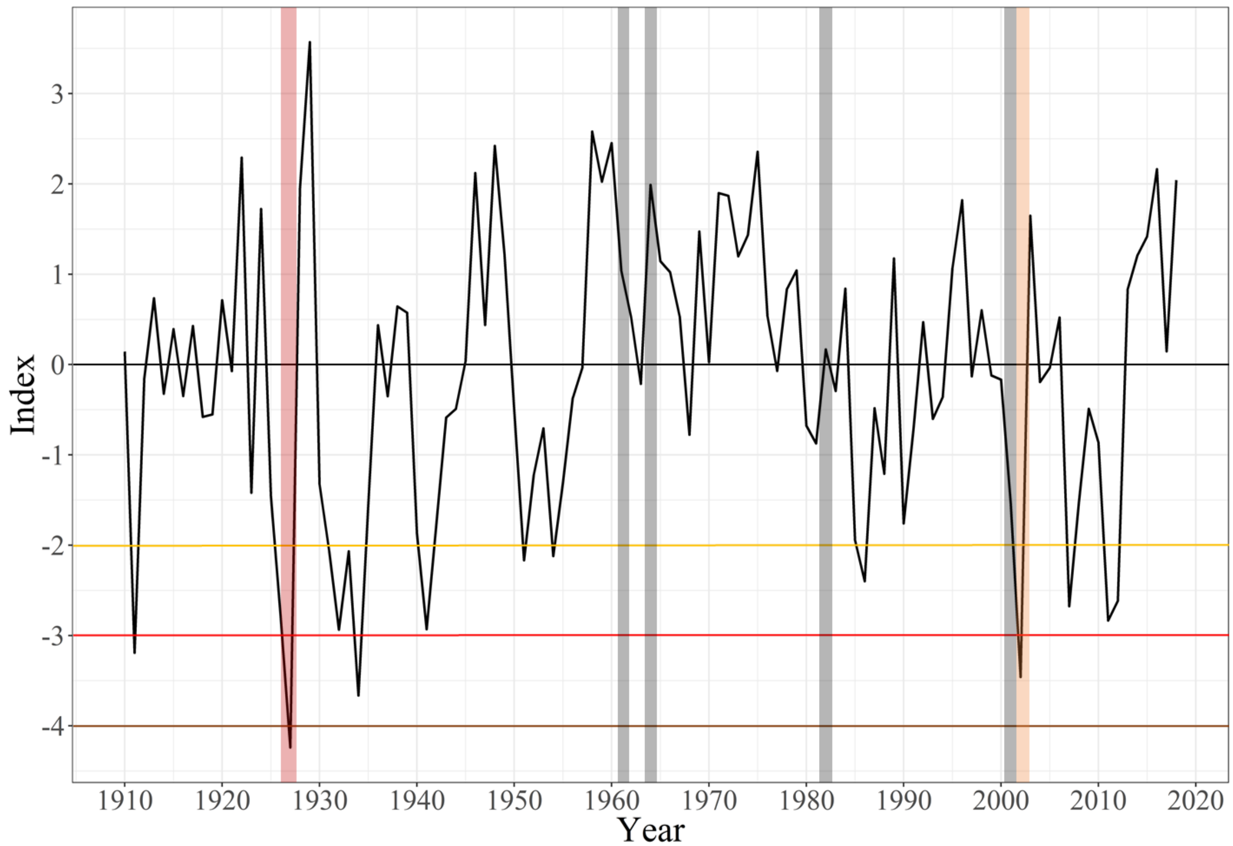

Fig. 9. Climate Division 6 annual average PDSI from NOAA (1910–2018). Grey boxes indicate highest percentage of trees suppressed for both suppression detection methods; years 1961, 1964, 1982, and 2001. The orange box is a severe drought with large suppression association. An extreme drought event is illustrated by a red box. Extreme drought is -4 or less (brown line), severe drought is -3 to -3.9 (red line), moderate drought is -2 to -2.9 (orange line) (Dai & National Center for Atmospheric Research Staff 2017)

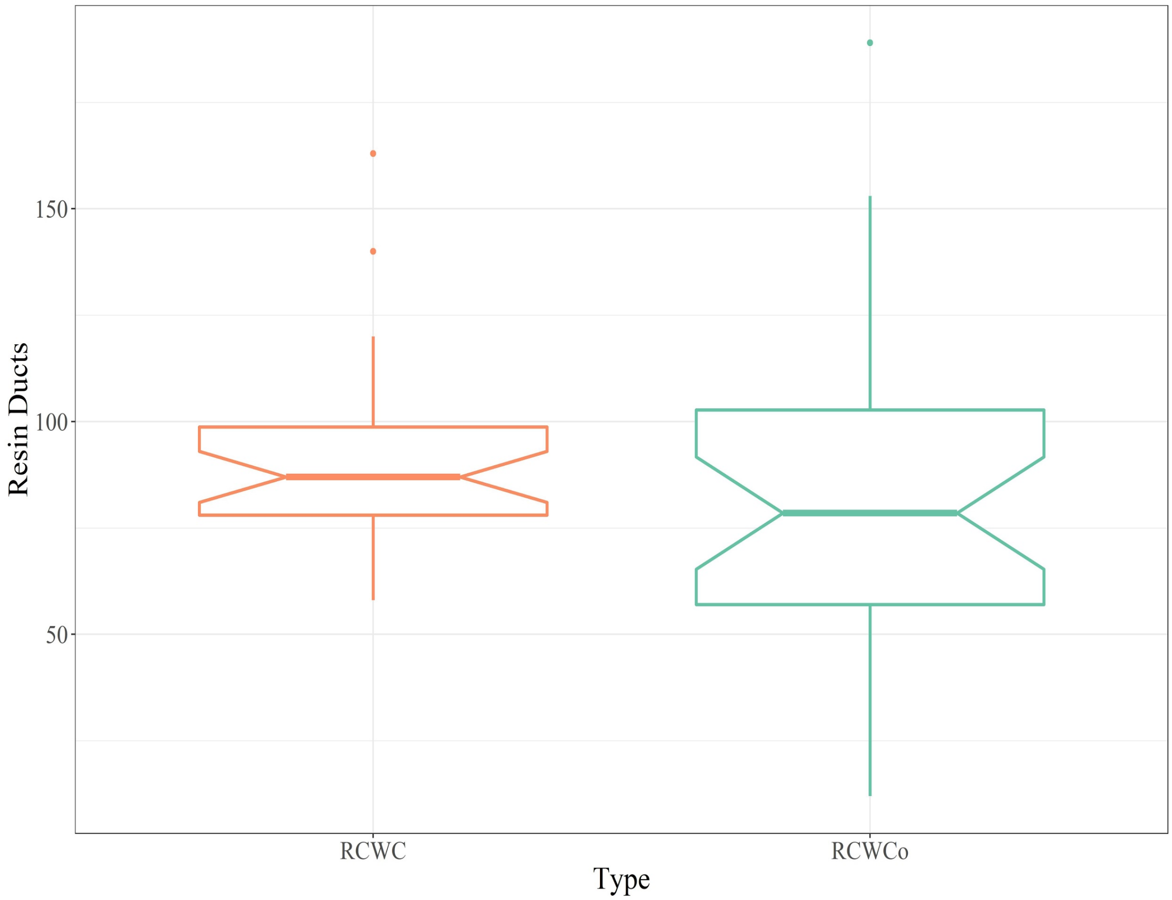

Fig. 10. Number of resin ducts 1950–2018 for RCWC (orange) and RCWCo (green) trees notches indicate 95% confidence interval

Vita

April Kaiser was born in Raleigh, NC to parents Steve Kaiser and Sonja Avena. She graduated from Needham Broughton High School in Raleigh, NC in June 2012. She then decided to move to the Blue Ridge Mountains to obtain her Bachelor of Arts in Biology with a double minor in Geography and Chemistry from Appalachian State University in Boone, NC. She graduated with cum laude honors in May of 2016. She returned to Appalachian State University to pursue her Master of Arts degree in Fall of 2017 and earned a Geographic Information Science graduate certificate in Spring 2019.During her graduate program, she was awarded two departmental scholarships, two travel awards from the Office of Student Research, and one travel scholarship from the Cratis D. Williams School of Graduate Studies. In August 2019, she graduated with a Master of Arts in Geography.